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Ecological studies of collembolan populations in a pine forest soil III. The life cycles and population dynamics of some surface dwelling species

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With 10 figures

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1. Introduction

Seasonal changes in numbers of Collembola have been studied in variety of habitats. Some workers have demonstrated how population abundance varies with environmental factors, such as soil humidity and temperature (Poole 1961, Dhillon & Gibson 1962, and Vannier 1970). Life history studies of field populations have been studied for some species, by analysing the size structure of population and the morphological characters of individuals, and have shown some interesting life history phenomena such as écomorphose, anhydrobiose and neutralization, which occur under adverse environmental conditions (Cassagnau & Raynal 1964, Cassagnau 1964, Poinsot 1968 and Ellis 1975). In spite of such increase in ecological studies of Collembola there is little information concerning the relation between life history events and seasonal changes in numbers (Nijima 1975, Tamura 1976, and Gregoire-Wibo 1976). Seasonal changes in numbers are closely related to the length of the life cycle and the number of generation per year of the constituent species, so that a synthesis of these two approaches is necessary to well understand the field population of Collembola under changing environmental conditions.

This paper, the fourth of a series dealing with the ecology of collembolan populations in a pine forest soil, describes the life cycles and population dynamics of four surface dwelling species which are similar in their life form and habitat preference in vertical distribution within a soil layer (Takeda 1973, 1976, and 1977).

2. Study area and methods

The study was carried out in a Japanese red pine forest (*Pinus densiflora* Sieb. et Zucc.) at Kamigamo Experimental station of Kyoto University, being situated about 12 km north of Kyoto city (35° 04′ N and 135° 43′ E). The details of study area have been published previously (Takeda 1976).

During the study period from July 1971 to May 1975, the mean air temperature ranged from 3.4 °C (January) to 28.5 °C (August). Soil temperature at 10 cm depth ranged from 4.7 °C (January) to 26.7 °C (August). The annual precipitation and evaporation were 1683 mm and 958 mm respectively. In this study area, high summer temperature with high evaporation and low water holding capacity of soil led to summer drought in 1971, 1972, and 1973, but in 1974 no summer drought occurred.

The soil samples were taken from the plot of 10×10 m^2 being divided into twenty subplots of 1×5 m^2. During the period from July 1971 to May 1975, sampling was made at about monthly intervals. Soil samples consisted of soil cores each 25 cm^2 in surface area and

4 cm deep (100 cc in volume) and the number of soil cores taken in each sampling occasion is shown in Fig. 2. Soil animals were extracted by a high gradient canister extractor (MACFADYEN 1961) at a constant temperature condition of 35 °C (Temp. in extractor cabinet). The period of extraction was six days. The extraction efficiency was determined by a comparison with a hand sorting method and nearly perfect extraction efficiency was obtained for the surface dwelling species (TAKEDA unpublished). The identification, counting and measurement were undertaken under binocular microscope with a micrometer.

3. Results

3.1. Size classes and sex ratio

Collembola have poorly marked life stages, are difficult to age and sex determination in the immature stages is not possible for the field populations. So the relationship between instar and size class is not readily obtainable as in other insects and some workers have used body length as a criterion of age (AGRELL 1941, MILNE 1961, JOOSSE 1969, NIIJIMA 1975 and TAMURA 1976). The validity of body length as a age criterion has been discussed by GREGOIRE-WIBO (1976).

The animals collected over the period July 1972 to May 1975 were grouped into size classes according to their body length. Beside the grouping of body length, the development of the genital orifice was examined for the animals collected during the period from July 1974 to May 1975. According to the morphology of the genital area, the following stages were distinguished; adult and juvenile for *Tomocerus varius* FOLSOM and *Sinella dubiosa* YOSII adult, immatured adult and juvenile stages for *Isotoma sensibilis* TULLB. and *Isotoma carpenteri* BÖRNER.

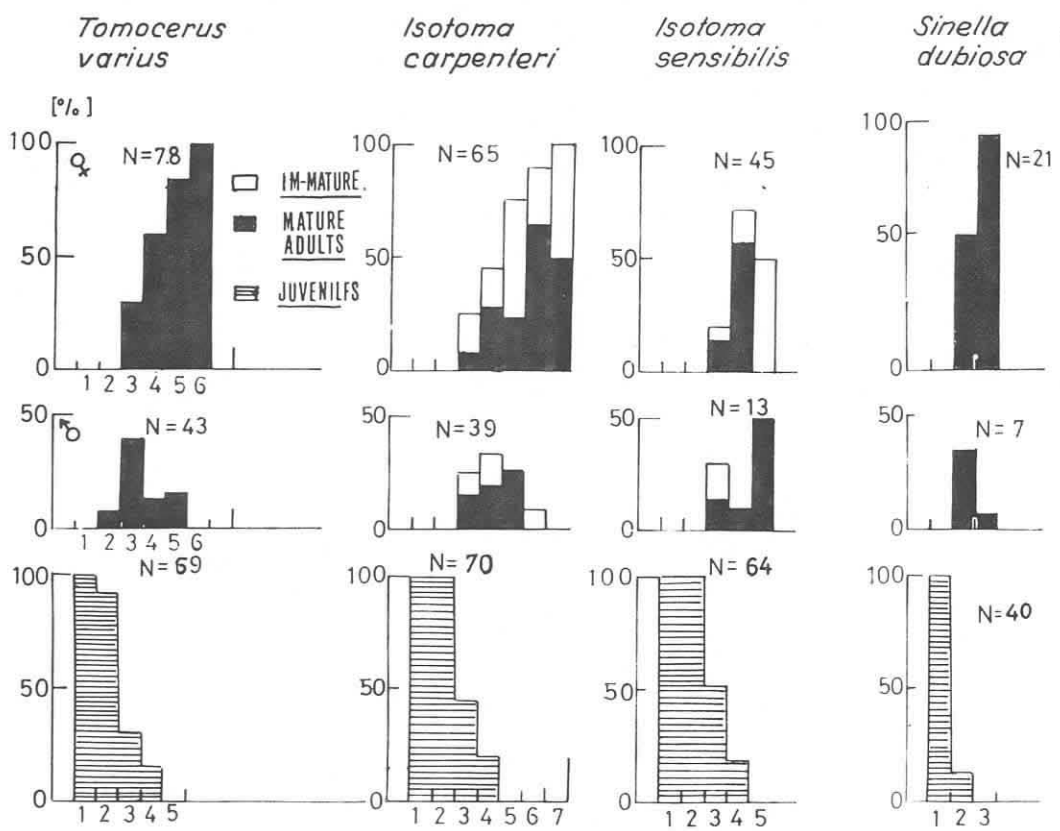

Fig. 1. Size distribution and sex ratio of four surface dwelling species. N indicates the number of individuals examined. Top: the percentage of adults (female), Middle: the percentage of adults (male), Bottom: the percentage of juveniles. The individuals collected were divided into following size classes; first ($\leqq$ 0.50), second (0.50—0.75), third (0.75—1.00), 4th (1.00—1.25), 5th (1.25—1.50), 6th (1.50—1.75) and 7th ($\geqq$ 1.75 mm).

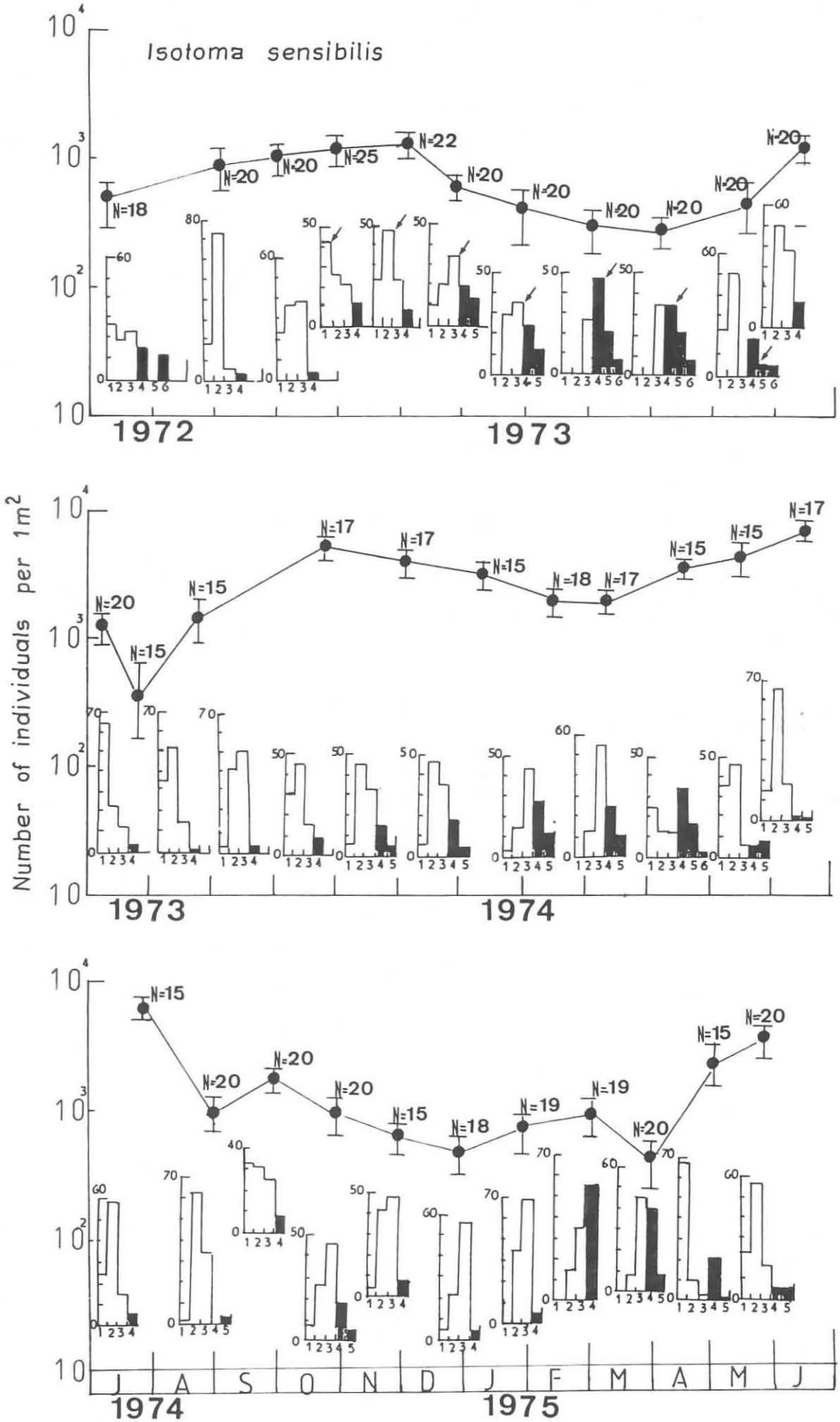

Fig. 2. Seasonal changes in size structures and numbers of *Isotoma sensibilis*. The size distribution was estimated from the monthly samples and in which the individuals represented by the unshaded portions of the histogram are juveniles and the shaded portions to the right represent adults. N indicates the number of soil cores taken in each sampling date.

The size distributions are shown in Fig. 1. The range of body length of adult females and males completely overlapped in the distribution of *I. sensibilis*, *I. carpenteri* and *S. dubiosa* but the mean length is longer in females than in males. In the distribution of *T. varius*, the range of body length of males was extended over the smaller size classes than that of females. The distribution of immature adults and mature adults were completely overlapped. The larger sized immature adults were collected during the period from late autumn to early spring and through the period mature adults were not collected.

The sex ratio was determined for the individuals collected during the period July 1974 to May 1975. The results are shown in Fig. 1. In all species examined, there was significant difference from a 1 : 1 sex ratio ($P < 0.01$). The biased sex ratio is a general phenomenon among natural populations of Collembola (Paclt 1956), but has not been explained. One of the explanations for the biased sex ratio may be the difference in mortality patterns of the sexes as shown in the uni-voltine species, *Tetracanthella sylvatica* Yosii (Takeda 1976).

3.2. Seasonal changes in size structure and population density

3.2.1. *Prefatory note*

The size structures and the population density through a three year period are shown in Fig. 2, 4, 6, and 8, in which the unshaded portions of the histograms are juveniles and shaded

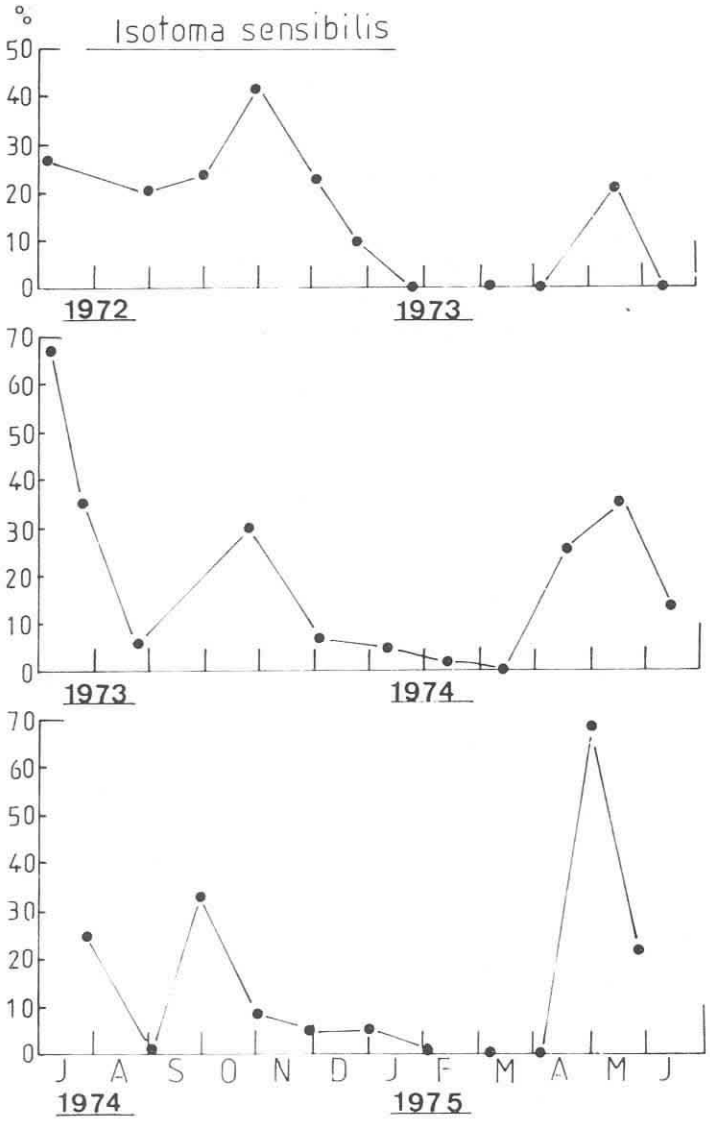

Fig. 3. Seasonal changes in breeding activity of *Isotoma sensibilis*, as shown by the seasonal changes in proportions of first size class individuals in the population.

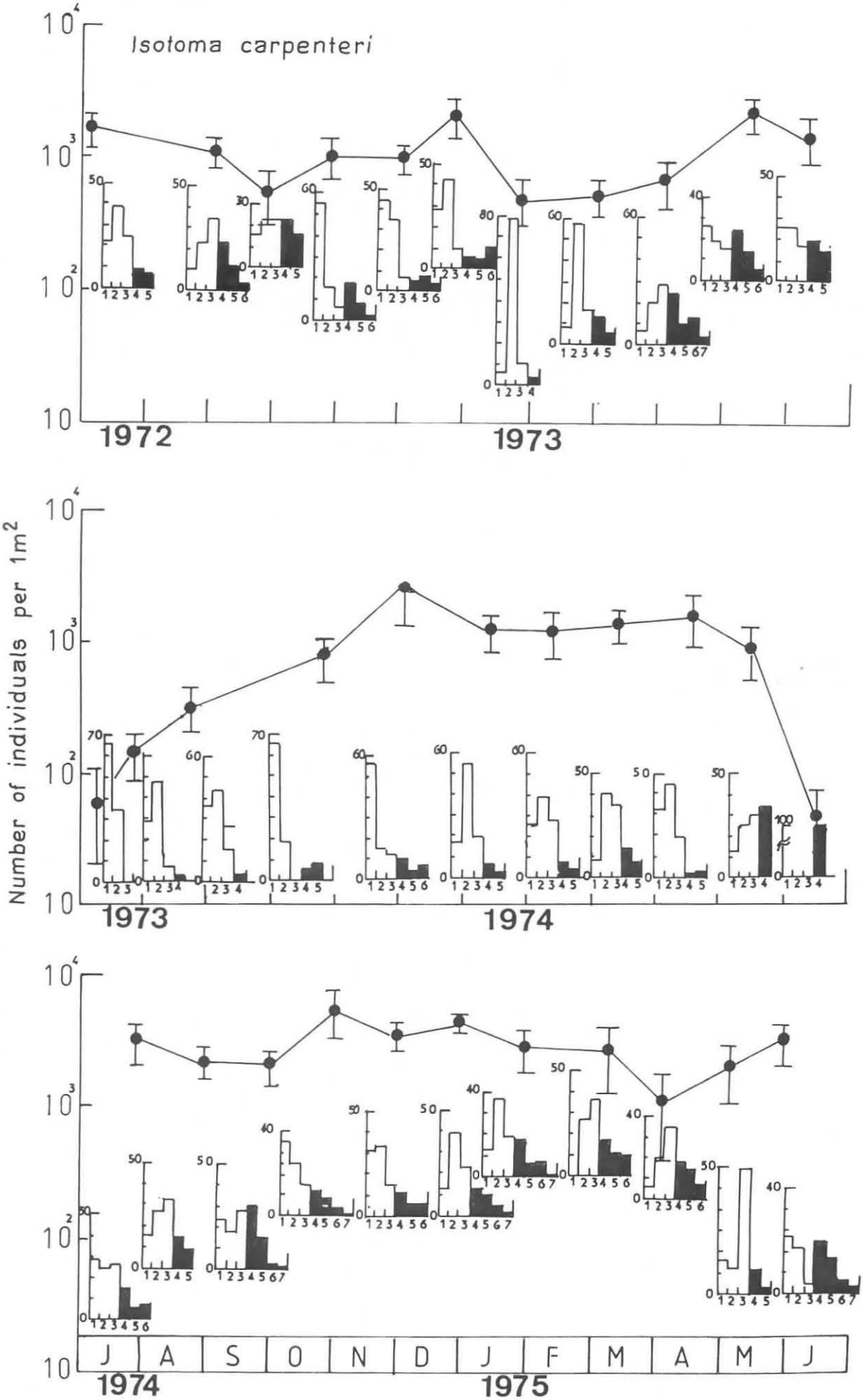

Fig. 4. Seasonal changes in size structures and numbers of *Isotoma carpenteri*.

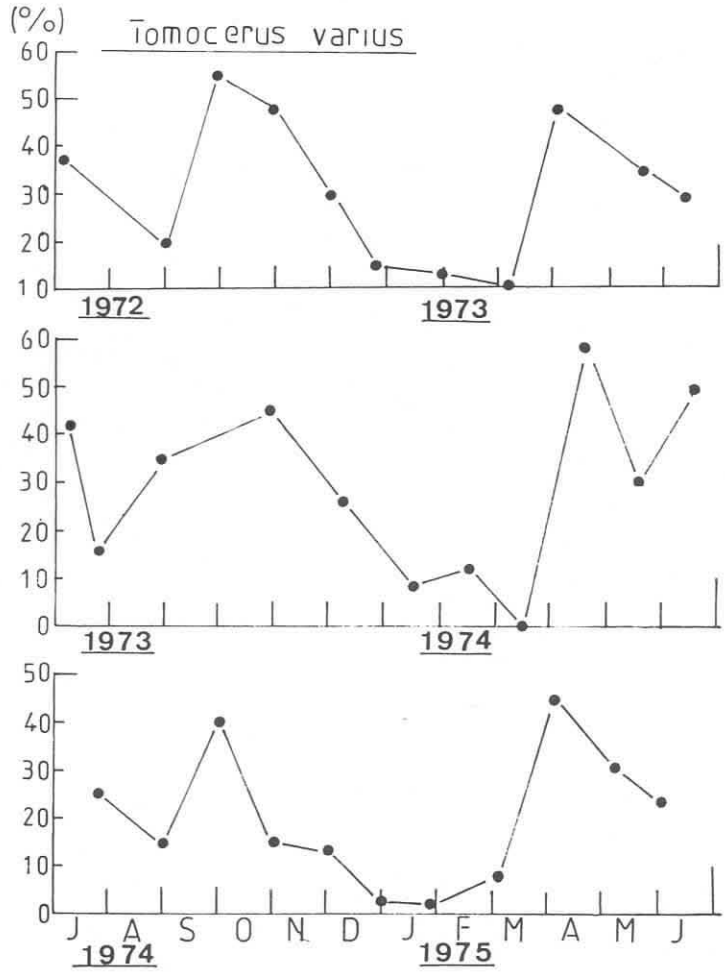

Fig. 5. Seasonal changes in breeding activity of *Tomocerus varius*.

portions to the right represent adults. This limit was determined from a consideration of Fig. 1.

The breeding activity in the populations was estimated from the counts of the percentages of first size class individuals in the total population (Fig. 3, 5, and 7.).

3.2.2. *Isotoma sensibilis*

This species is cosmopolitan and xerophil surface dwelling form (GISIN 1948, USHER 1969, VAN DER DRIFT 1970, and TAKEDA 1977). The mean monthly density was ranged 280 to 6175 with a mean 1792 per m^2. The mean annual density was 1529, 751, 3399, and 1489 per m^2 for the first, second, third and fourth annual cycles respectively.

The life cycle was estimated by following the shift of peak in the size distribution. Fig. 3 indicates that the recruitment took place mainly in three waves occurring in July/August, late October and May, as shown by the increase of the portion of the smallest size class in the population. The generation appeared in July/August (summer generation) grow into adult stage by October and survived to early winter. The generation in late October (autumn generation) grew during autumn, winter and spring and attained adult stage by the following spring. The breeding of the autumn generation took place after over wintering when soil temperature exceeded about 5—10 °C in early spring. The generation in May (spring generation) grew rapidly during spring and early summer and attained the adult stage by mid summer.

3.2.3. *Isotoma carpenteri*

This species is white in body colour, having reduced eyes and is distributed mainly in the boundary between litter and F layer (TAKEDA 1977). This species is endemic in Japan and numericaly abundant in forest soils (NIIJIMA 1975).

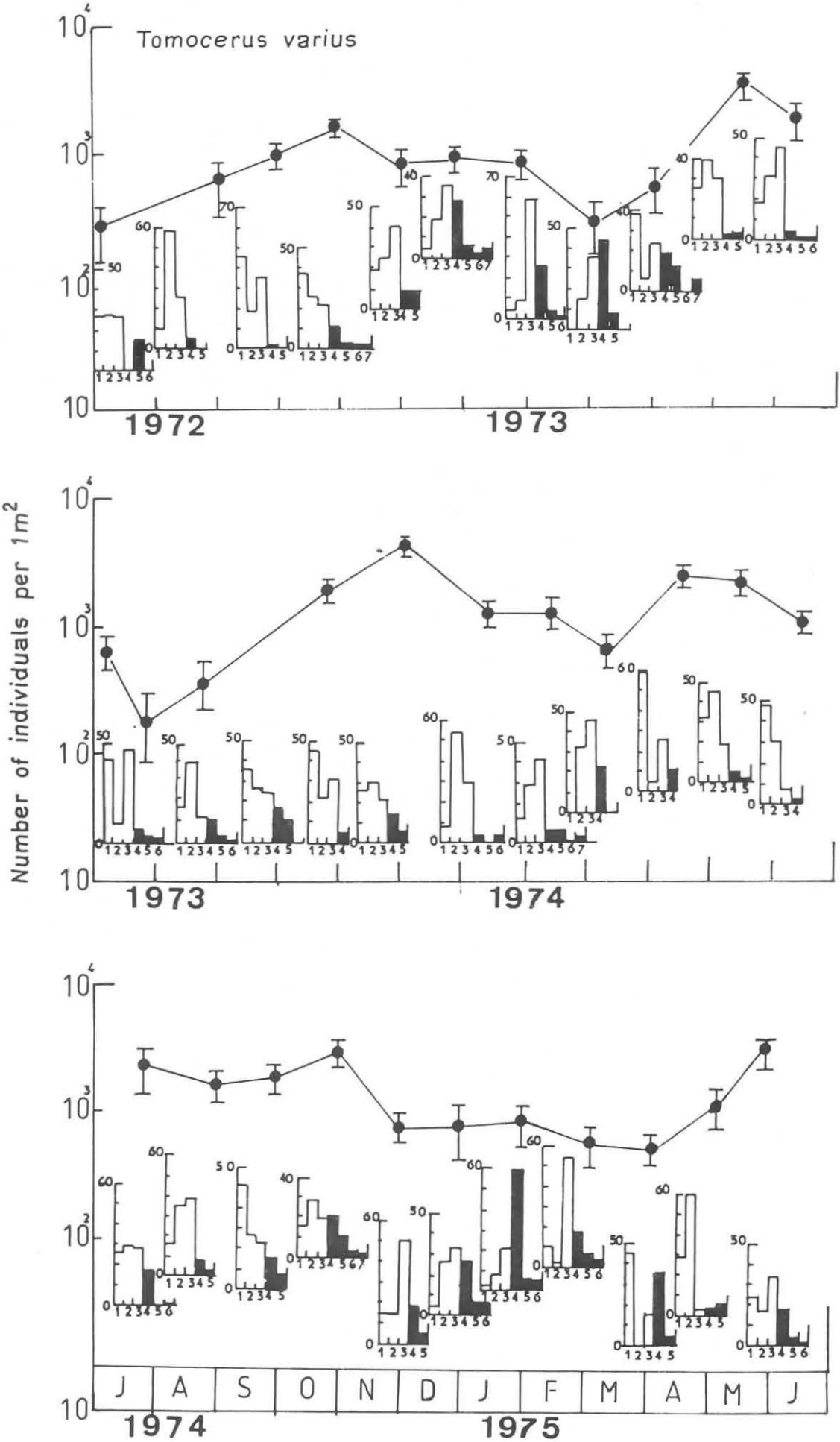

Fig. 6. Seasonal changes in size structures and numbers of *Tomocerus varius*.

The mean population density ranged from 47 to 5161 with a mean density of 1529 per m^2. The annual population density was 963, 1240, 934, and 2978 per m^2 for the first, second, third, and fourth annual cycles respectively. The mean population density of 1529 per m^2 over the study period was a comparable value to that of *I. sensibilis* with a mean density of 1937 per m^2. But it was noted that *I. carpenteri* was more abundant in the fourth annual cycles during which there was no summer drought in 1974. *I. sensibilis* was less abundant in the fourth annual cycle and more abundant in third annual cycles when summer drough was exceptionally severe in 1973. This difference in annual population density may reflect the different humidity preference between the species.

Fig. 4, 7 show that the recruitment extended over a year but the main period was during July, Oct/Nov. and May. The recruitment of the autumn generation extended over a longer period than the other species.

3.2.4. *Tomocerus varius*

This species is a common surface dwelling species in Japanese forest soils and is the most abundant species amongst Tomoceridae. The distribution is endemic and extends from lower land to high alpine zone in Japan (Niijima 1975).

During a period of four years, the population density ranged from 92 to 4545 with a mean of 1252 individuals per m^2. The mean annual density was 618, 1144, 1640 and 1605 per m^2. Through the study period, the annual density showed an increase. There was no remarkable difference in annual population density between the third and fourth annual cycles as observed in the cases of *I. sensibilis* and *I. carpenteri*.

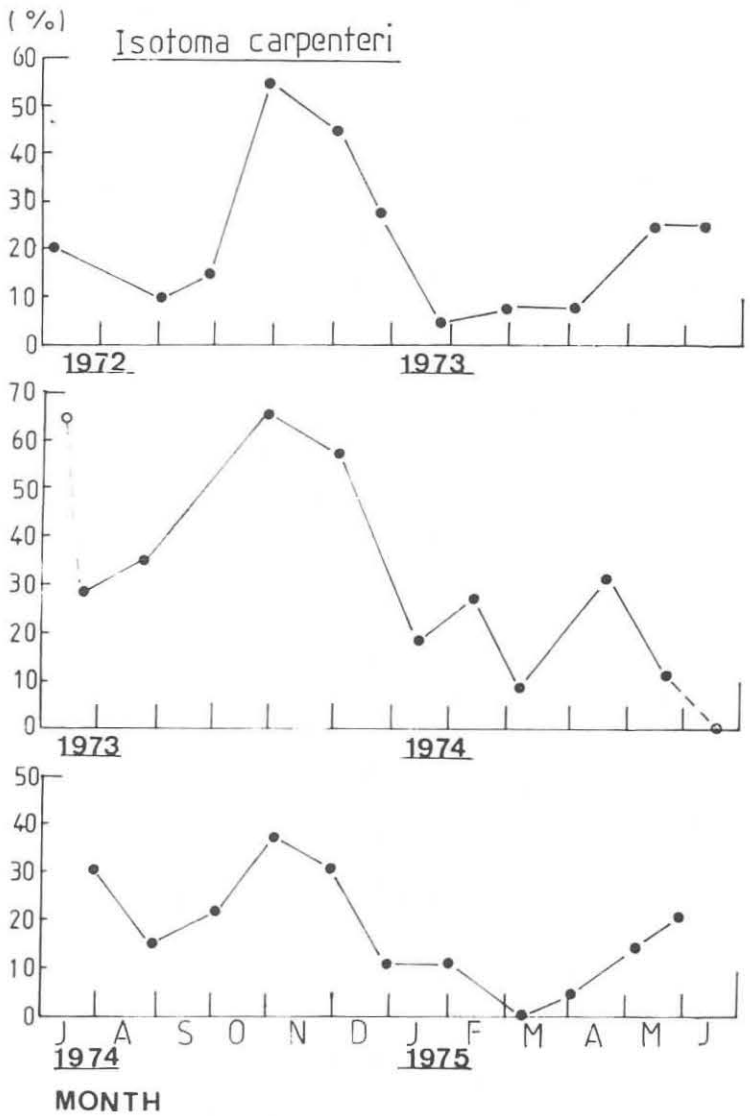

Fig. 7. Seasonal changes in breeding activity of *Isotoma carpenteri*.

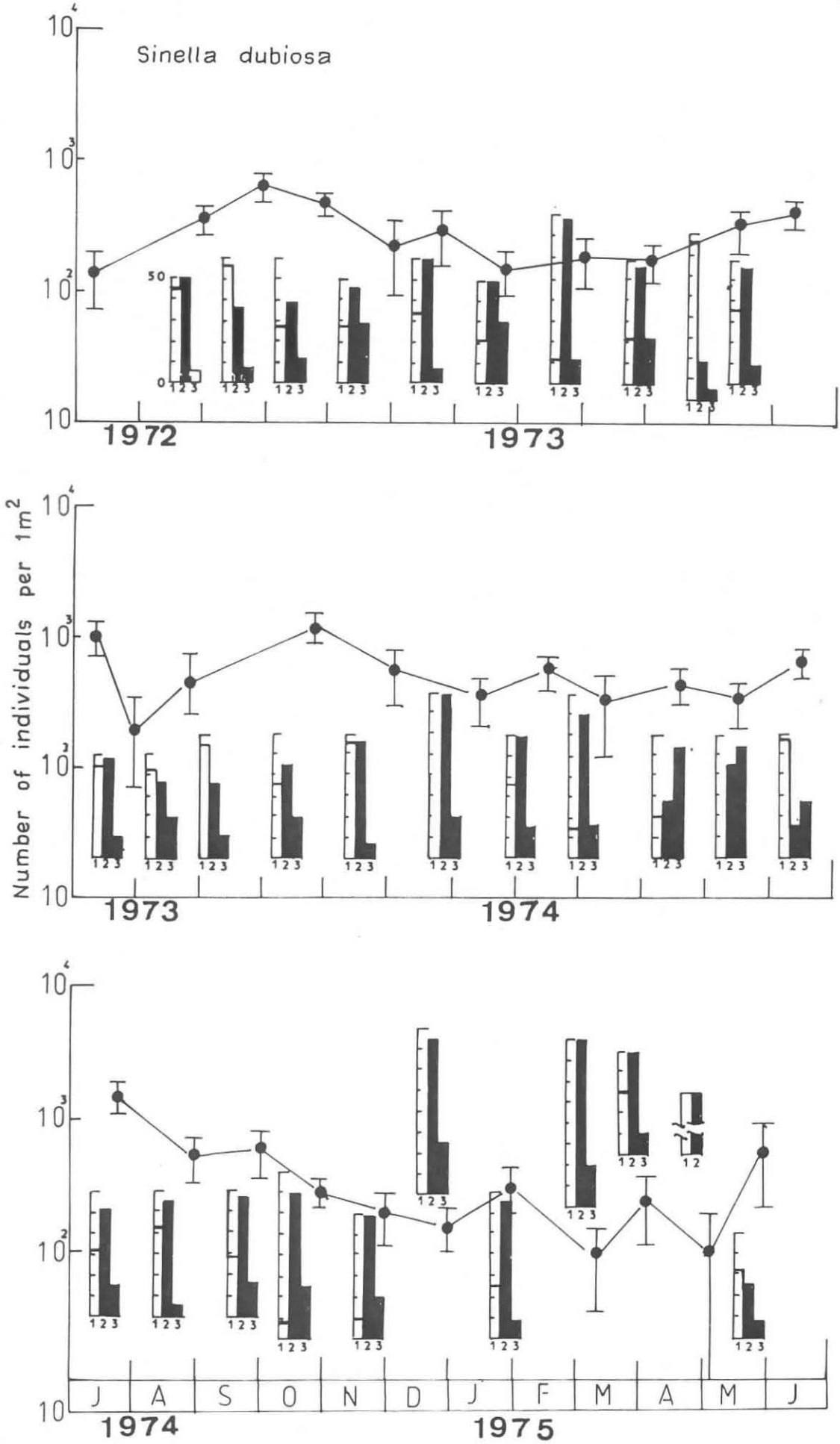

Fig. 8. Seasonal changes in size structures and numbers of *Sinella dubiosa*.

3.2.5. *Sinella dubiosa*

There were three main recruitment periods in a year, i.e. July, Oct, and May. During winter there was less or no first size class individuals in the population and this suggests that recruitment had not occurred during the period.

The life cycle pattern was similar to those of *I. sensibilis*, and *I. carpenteri*.

This species is endemic but morphologically similar to European species *Sinella höfti* SCHÄFER. The vertical distribution range is similar to that of *I. carpenteri*.

The mean population density ranged from 89 to 1400 with a mean of 432 per m^2. The annual population density was 430, 301, 604 and 391/m^2 in the first, second, third, and fourth annual cycles respectively. The population density was high in the third annual cycle when the summer drought was severe and this trend was similar to that of *I. sensibilis*.

The population density was lower so that the life cycle was not well demonstrated. During winter there were portions of the smallest size class in the population in 1974, and 1975, this may suggest the possibility of winter breeding.

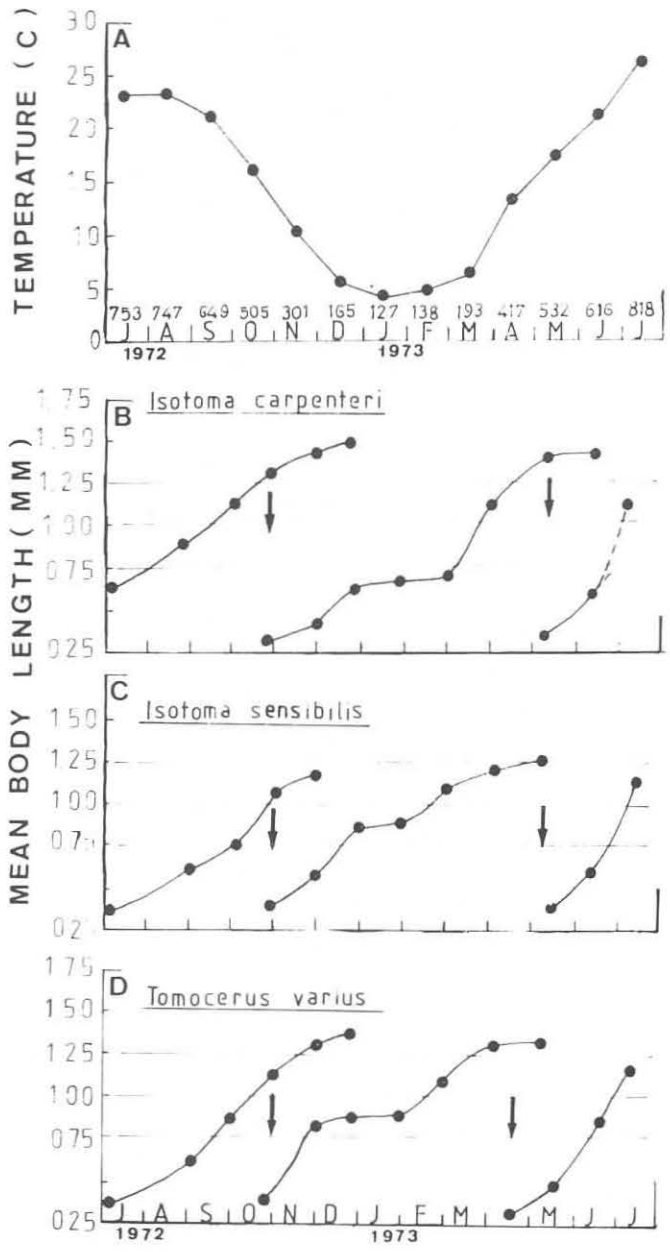
TEMPERATURE (C)
A
753 747 649 505 301 165 127 138 193 417 532 616 818
J A S O N D J F M A M J J
1972
1973
MEAN BODY LENGTH (MM)
B Isotoma carpenteri
C Isotoma sensibilis
D Tomocerus varius
MONTH

Fig. 9. Growth curve of mean body length of *I. sensibilis*, *I. carpenteri* and *T. varius* and seasonal changes in soil temperature at 10 cm depth. Growth curves were estimated from the shift of peak in size distribution.

3.3. Growth analysis

Recruitment continued throughout the year except in winter but variations in the breeding gave a succession of generations that could be followed from peak to peak in the size distributions.

Fig. 9 shows the mean body length for each generation plotted against the sampling date, with the seasonal changes in soil temperature at 10 cm deep.

The growth pattern of the summer generation was not different among the species examined and was represented by the rapid growth period from June to October. After the breeding in October the growth rate decreased. Recruitment of the autumn generation occurred when the summer generation attained about 80 percent of its fully grown size. The growth pattern of the autumn generation was represented by the early growth in late

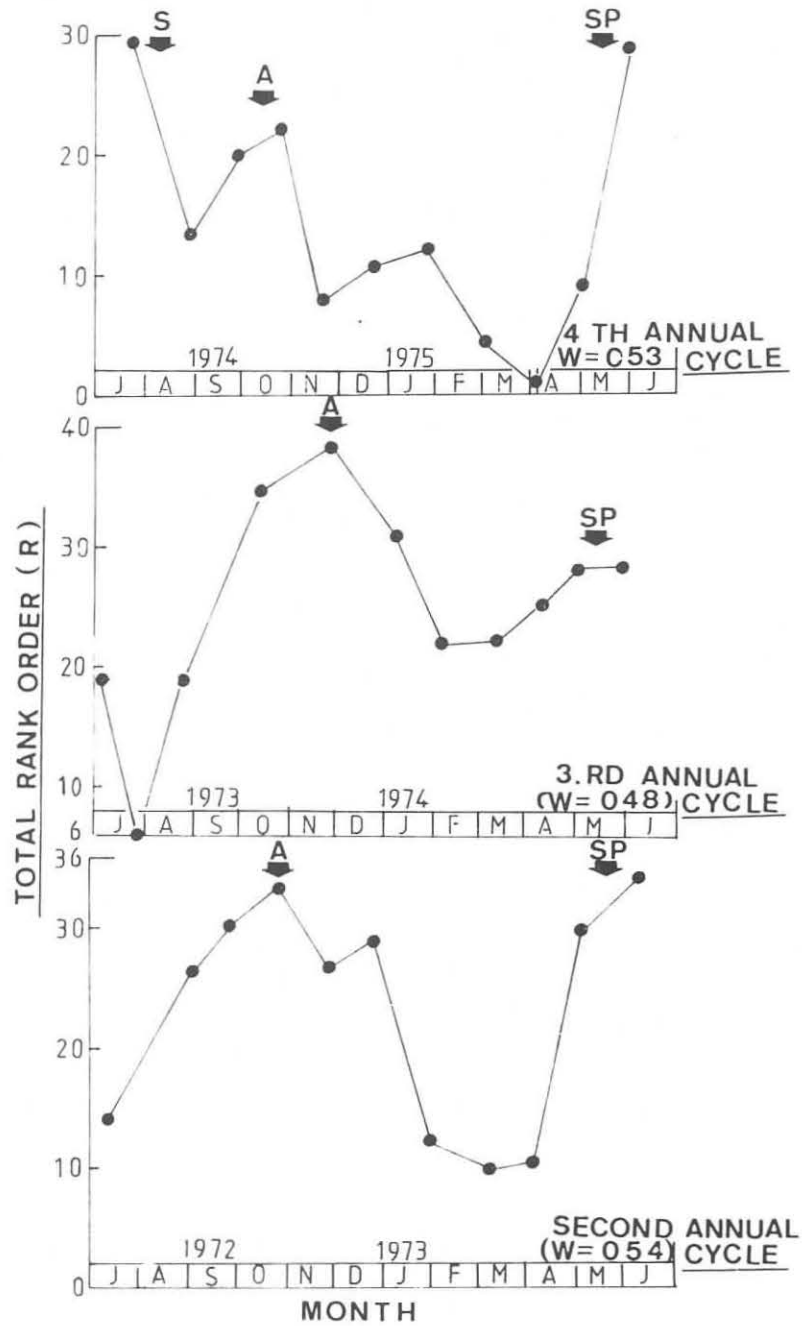

Fig. 10. Common seasonal trends in population abundance of four species populations were represented by the total rank order. Arrow indicates the population peak.

autumn and early winter, the retard of growth during winter and the spring growth. Through the early growth, the mean body length of *I. sensibilis*, *I. carpenteri* and *T. varius* attained about 70, 50, and 70 percent of their full grown size respectively and *T. varius* and *I. sensibilis* also attained their adult size by the winter arrestation of growth. The breeding of the autumn generation took place in the spring when they attained their full grown size. The individuals of spring generation showed a rapid growth during spring and early summer and attained their full grown size by early summer.

3.4. Comparison of the seasonal abundance between species

The Kendall's coefficient of concordance was computed to determine the agreement of seasonal abundance between the four species (SIEGEL 1956). The coefficient of concordance (W) expresses the degree of agreement among the seasonal abundances of four species. The value of W is 0.54, 0.48, and 0.53 for the second, third, and fourth annual cycles respectively. The test of significance indicates that the value of W is significant for all cases examined at $P = 0.05$ level. When the agreement of seasonal abundance among species is significant, the total rank order can be used to represent the common pattern of the seasonal abundance. The total rank order is shown in Fig. 10. The figure indicates that the four species show two peaks occurring in Oct. and May/June in the second and third annual cycles, and three peaks occurring in July, Oct. and May in the fourth annual cycle.

4. Discussion

The number of generation a year in a species depends upon the life span as well as the environmental conditions, so it is reasonable to restrict the comparison of life cycles to same species or genus groups. There are few studies on the life cycles of Collembola with which the present results can be compared. It appears from the results that the species studied have three generations a year (in *S. dubiosa*, the life cycle has not yet been demonstrated) and the life cycle patterns were not different from species to species. Recruitment usually took place through they ear except in winter, but may be largely confined to certain months: July, Oct., and May. The generation appearing in spring, summer and autumn took about 3, 4, and 6 month to attain their full grown size, but the autumn generation had retarded growth during the winter, about two months, so the life span of each generation is not so different. HALE (1966) found that most species of Collembola in high moor land in England had only one or at the most two generations a year and *I. sensibilis* had one generation a year with the period of maximum oviposition in spring. FJELLBERG (1975) found that the ten species of Collembola in a tundra ecosystem in an alpine region in southern Norway were grouped into three types, i.e. a one, two and three year life cycle, the one year cycle group consisted of *I. anglicana*, *I. viridis*, *I. notablis*, *I. olivacea* and *I. violacea*. In a pine forest in Netherland, JOOSSE (1969) studied life cycles and population dynamics of surface dwelling species and estimated two generations for the population of *Lepdocyrtus cyaneus*, *Orchesella cincta*, *Entomobrya nivalis* and *Isotoma viridis* and three generations a year for *T. minor* being hygrophilic species. TANAKA (1970) found that *I. trispsinata* had six generations a year in southern part of Japan. The number of generations a year estimated in this study is reasonable in a comparison with other studies. A comparison of life cycles studied in various habitats suggest that the number of generations a year has closely related to the temperatures regime in the habitats. Hence even in same species the number of generations a year changes according to the temperature regime of habitats where the species lives, as shown by the cases of *I. viridis* and *I. sensibilis*.

The difference of life cycle patterns between the same species living in different climatic conditions may be attributed to the difference of the duration of growth period in a year and the growth rate during the growth periods which relates with temperature, as have been demonstrated in experimental conditions.

The interruption of breeding and retardation of growth were observed during winter when temperature decreased below about 10 °C and resumed in spring when the temperature

raised to about 5—10 °C. USHER (1970) found that the recruitment of new individuals occurred through the year but was most intensive during April to May when the soil temperature raised to about 5 °C. NIIJIMA (1975) also found that in a temperate warm forest in Japan, *T. varius* showed a retardation of growth during winter and the recruitment of newly hatched individuals and growth commenced in May when soil temperature raised to about 7 °C. These results well agree with the present results. AGRELL (1941) and TAMURA (1976) reported that Collembola were relatively resistant to low temperature and could live in frozen soils. So the low temperature observed in this study area and NIIJIMA's area seems not to be lethal for the survival of the populations. The interruption of breeding and retardation of growth during winter may be regarded as adaptive life strategies, in escaping the breeding in adverse environmental conditions and in having a synchronous breeding in spring when environmental conditions become favorable.

Seasonal changes in population abundance are determined by the combinations of natality and mortality patterns in a population in which migration is not an important factor for the population changes. JOOSSE (1969) examined the migration of Collembola by pit-fall trap methods and concluded that migration was not an important factor to explain the population changes observed. This may be explained by the physiological character of Collembola, because Collembola usually require high humidity (over 90 % in R.H.). So the migration seems to be less important for the population changes in Collembola living in the soil layer. The population changes observed in this study may be explained by the balance of mortality and natality. The natality pattern through a year was estimated by the breeding activity (Fig. 3, 5 and 7). The pattern of breeding activity was not different from year to year and was represented by more or less synchronized occurrence of juveniles in July; Oct./Nov. and May/June. A comparison of the breeding activity and the population abundance through a year reveals closely parallel trends in the fourth annual cycle when no summer drought occurred but the summer peak in breeding activity was suppressed by mortality in 1972, and 1973 when summer drought occurred. Therefore, for the surface dwelling species the pattern of seasonal changes in population abundance reflects more or less those of breeding activity as long as mortality does not suppress the breeding patterns as observed in the fourth annual cycle. But adverse environmental conditions affect mortality and can override the relation between natality and seasonal abundance patterns as observed in the second and third annual cycles.

GLASGOW (1939) and WEIS-FOGH (1948) have shown that climatic factors may be causally responsible for seasonal changes in population abundance. It seems to be accepted that the population decrease is attributed to adverse environmental conditions such as cold in winter and drought in summer and the increase of population to ideal moisture and temperature conditions. However little is known how such environmental factors affect populations. The life span of surface dwelling species is relatively long as shown in the results, so that the rapid population increase due to the increase of natality in response to the changes in environmental conditions are not expected for these populations. While the mortality in response to the adverse environmental conditions and predation would directly affect the population changes without time delayed response, as shown in the population decrease in summer 1973, and 1974.

5. Acknowledgements

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6. Summary

Seasonal changes in numbers and age-structures of four species of Collembola, *Isotoma sensibilis*, *Isotoma carpenteri*, *Tomocerus varius*, and *Sinella dubiosa* were studied in a pine forest near Kyoto, Japan, over a period of four years. The species studied had three generations per year (in *S. dubiosa*, life cycle was not yet been clearly demonstrated) and the pattern of life cycle was similar among

the species studied. Recruitment usually took place through a year except winter but was largely confined to certaine month, July, Oct./Nov. and May/June. The generation appeared in spring, summer and autumn took about 3, 4 and 6 months to attaine their full grown size. But autumn generation had a retard of growth during winter, so the life span of each generation was not different.

The population studied consisted of 4 species and the trends in seasonal abundance were similar between species. The common trends in seasonal abundance showed two population peaks occuring in Oct./Nov. and May/June in the second and third annual cycles and three peaks occuring in May/June, July and Oct./Nov. in the fourth annual cycle.

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